The Ferns of Elden Mountain, Arizona

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Elden Mountain, located immediately northeast of Flagstaff in north-central Arizona, is an unusual volcanic peak with a diverse fern flora. The earliest pteridophyte collections from the area are those taken by L. N. Goodding in 1913. Whiting and Bradey collected extensively on the mountain during the 1930's and were apparently the first to encounter *Asplenium adiantum-nigrum* in 1935. In a short article discussing the occurrence of this species in Arizona, Wherry (1941) mentioned five other ferns casually observed during a visit to the locality. Phillips (1946, 1947) listed five additional taxa for the mountain, bringing the number of reported species to 11. The flora of Elden Mountain received little attention during subsequent years, and much of the area remained unexplored when a forest fire inflicted heavy damage in June, 1976. Concerned about the fate of several rare species, I began a comprehensive survey of surviving fern populations in 1978.

Elden Mountain is a massive dacite dome located near the center of the San Francisco volcanic field. Although precise dates are not yet available, geologists agree that the dome was formed sometime during the last million years (Kluth & Kluth, 1974). The dacitic magma was quite viscous, and well-defined lava flows are evident on all slopes. Juxtaposition of lava flows created a highly complex topography, and erosion has produced innumerable cracks and crevices that provide favorable habitats for a variety of unusual plants. The elevation at the base of the mountain averages 7000 feet; the summit falls just short of 9300 feet.

A lengthy meteorological record is available for nearby Flagstaff at 6900 feet elevation (Sellers & Hill, 1974); much of the general climatic data is applicable to Elden Mountain. At Flagstaff, the lowest average monthly temperature (27.3° F) occurs in January, the highest (65.5° F) in July. The mean frost-free period extends from June 8 to September 26, a total of 110 days. Annual precipitation averages 18.31 inches, and seasonal rainfall patterns are distinctly bimodal. The greatest amount of rainfall occurs in July and August, when storm systems enter the region from the Gulf of Mexico. Pacific-based storms produce a second precipitation peak in January and February, but the months of May, June, and November are characterized by drought, which was a major factor in the disastrous fire of 1976.

The distinct vegetation zones observed on the San Francisco Peaks (Merriam, 1890) are all but absent on Elden Mountain. Abrupt topography brings diverse habitats into close proximity, and plant associations on the peak are extremely complex. The areas surrounding the base of the mountain are dominated by *Pinus ponderosa*, which is frequently associated with *Quercus gambelii*. South-facing slopes exhibit a dense cover of *Cercocarpus montanus*, *Berberis fremontii*, *Juniperus deppeana*, *J. osteosperma*, *Pinus edulis*, *Opuntia phaeacantha*, and *Yucca baccata*. The northern slope and crest of the mountain support a mixed conifer forest in which *Pseudotsuga menziesii*, *Abies concolor*, and *Pinus flexilis* dominate. Small meadows and stands of *Populus tremuloides* occupy a limited area near the summit. Some areas show a haphazard mixture of all the species mentioned above.

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METHODS AND MATERIALS

The data presented herein result from intensive fieldwork undertaken between February, 1978 and March, 1983. Considering the size and complexity of Elden Mountain, it would be unwise to suggest that the pteridological survey is complete. However, most suitable habitats have been examined, and recent visits to the area have failed to yield additional, unreported species. Detailed field notes were kept concerning the distribution and habitat preference of each taxon, and population estimates were derived through a census of individual adult plants. Ten mature sporangia were gathered from each species, and their contents were examined in glycerol to determine spore number. Most cytological materials were field fixed in May and June using Farmer's solution (3 parts ethanol: 1 part glacial acetic acid). Plants not demonstrating the proper meiotic condition were transferred to a greenhouse to stimulate the production of fertile fronds. Fixed sporangia were hydrolyzed for approximately 15 minutes in 1N HCl prior to staining with aceto-orcein. Hoyer's solution was used as the squashing and mounting medium in all chromosome preparations. Counts were derived from cells at late diplotene or diakinesis and were documented using a camera lucida. Voucher specimens for all phases of this study have been deposited at the Deaver Herbarium, Northern Arizona University (ASC).

RESULTS AND DISCUSSION

All fern species previously reported for Elden Mountain were relocated during this survey, proving that none was lost as a direct result of the 1976 fire. In fact, the number of recognized species was nearly doubled by the discovery of two unreported herbarium collections and seven taxa new to the mountain. None of the additions were found in fire-damaged areas, and it is apparent that they have existed on the mountain for quite some time. Nearly all are characterized by low population densities, which may explain why they were overlooked by previous collectors. The survey has revealed that the Elden Mountain fern flora comprises 20 species representing 11 genera. Chromosome counts have been obtained for 15, and spore count data are available for all but one.

Adiantum pedatum L.—Discovered in 1979, the colony consists of ca. 25 plants growing on the western slope at 8100 ft elevation. The plants are confined to a small area of permanent seepage on the back wall of a narrow cliff recess. The length/width ratio of the laminae is unusually high compared to other Arizona collections, but elongate fronds are occasionally observed throughout the range of the species. Mature sporangia consistently produced 64 normally developed spores.

Asplenium adiantum-nigrum L.—The Elden Mountain population comprises at least 100 individuals scattered over the southern and eastern slopes at 7100–8100 ft elevation. The plants favor shaded cracks, crevices, and ledges on relatively dry, south-facing cliffs. All sampled sporangia yielded 64 normal spores, and a chromosome count of $n = 72$ II (*Fig. 1A*) agrees with previous determinations from Europe and Colorado (Shivas, 1969) Colorado specimens were originally described as *Asplenium andrewsii* A. Nels., and Chihuahuan collections provided the type materials of *A. chihuahuense* J. G. Baker and *A. dubiosum* Davenp. (Knobloch & Correll, 1962). The proliferation of names in the New World resulted from the

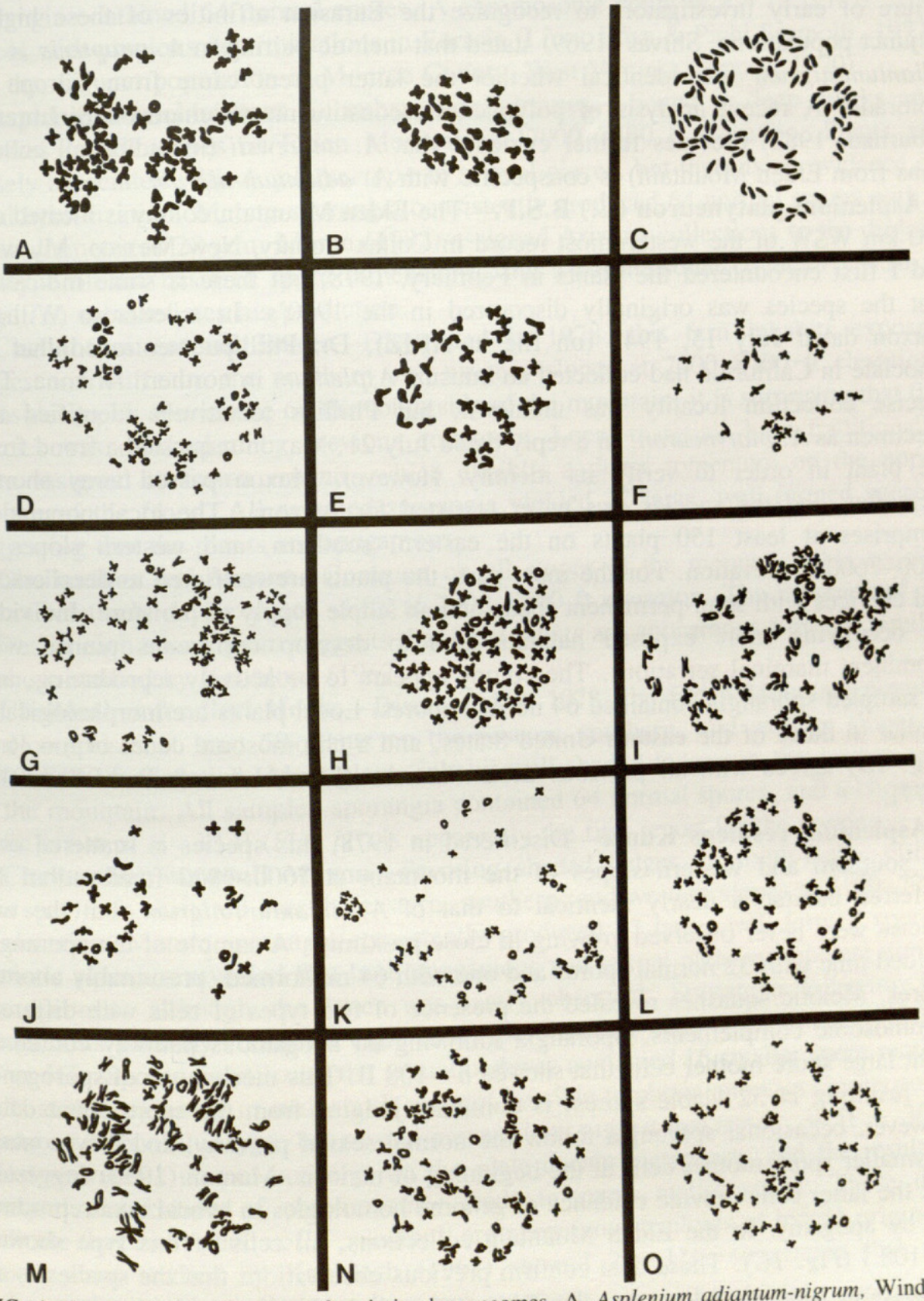

FIG. 1. Camera lucida drawings of meiotic chromosomes. A. *Asplenium adiantum-nigrum*, Windham 351. B. *A. platyneuron*, Windham 394. C. *A. resiliens*, Windham 400. D. *A. septentrionale*, Windham 393. E. *A. trichomanes*, Windham 397. F. *Cheilanthes fendleri*, Windham 26. G. *C. wootonii*, Windham & Yatskievych 266. H. *Cystopteris* cf. *tennesseensis*, Windham & Windham 319. I. *Dryopteris filix-mas*, Windham 395. J. *Pellaea truncata*, Windham 149. K. *P. wrightiana*, Windham 396. L. *Polypodium hesperium*, Windham 392. M. *Polystichum scopulinum*, Windham 398. N. *Woodsia mexicana*, Windham 402. O. *W. oregana*, Windham & Windham 253.

failure of early investigators to recognize the Eurasian affinities of these highly disjunct populations. Shivas (1969) stated that meiotic pairing in *A. onopteris* × *A. adiantum-nigrum* was identical whether the latter parent came from Europe or Colorado. A recent analysis of polyphenolic constituents (Richardson & Lorenz-Liburnau, 1982) provides further evidence that *A. andrewsii* (including all collections from Elden Mountain) is conspecific with *A. adiantum-nigrum*.

Asplenium platyneuron (L.) B.S.P.—The Elden Mountain colony is located ca. 600 km WSW of the westernmost record in Colfax County, New Mexico. My wife and I first encountered the plants in February, 1978, but there is some indication that the species was originally discovered in the 1940's. In a letter to William Maxon dated July 15, 1947 (on file at ARIZ), Dr. Phillips mentioned that an associate in California had collected an unusual *Asplenium* in northern Arizona. The precise collection locality was unknown, but Phillips tentatively identified the specimen as *A. platyneuron*. In a reply dated July 21, Maxon requested a frond from the plant in order to verify its identity. However, Maxon passed away shortly thereafter, and the species was never reported for Arizona. The local population comprises at least 150 plants on the eastern, southern, and western slopes at 7000–7600 ft elevation. For the most part, the plants are restricted to deep cracks and crevices with semi-permanent shade and an ample supply of moisture. Individuals occupying more exposed habitats tend to develop coriaceous pinnae with prominent marginal serrations. The colony appears to be actively reproducing, and all sampled sporangia contained 64 normal spores. Local plants are morphologically similar to those of the eastern United States, and a chromosome count of $n = 36$ II (*Fig. 1B*) agrees with all previous determinations (Löve, Löve & Pichi Sermolli, 1977).

Asplenium resiliens Kunze—Discovered in 1978, this species is scattered over the southern and western slopes of the mountain at 7000–7800 ft elevation. Its preferred habitat is nearly identical to that of *A. adiantum-nigrum*, but the two species were never observed growing in close proximity. A sample of ten sporangia yielded nine with 32 normal spores and one with 64 malformed, presumably aborted spores. Meiotic squashes revealed the presence of two types of cells with different chromosome complements. Sporangia following an apogamous pathway contained eight large spore mother cells that showed $n = 108$ II. This mechanism of sporogenesis, resulting in 32 viable spores, is dominant judging from the spore count data. However, occasional sporangia follow the normal sexual pathway, and they contain 16 smaller spore mother cells at the beginning of meiosis. Manton (1950) suggested that the latter cells provide evidence of genome homologies in hybrid taxa reproducing by apogamy. In the Elden Mountain collections, all cells of this type showed $n = 108$ I (*Fig. 1C*). These data confirm previous observations that the species is an apogamous triploid and suggest that the putative diploid and tetraploid parents were not closely related.

Asplenium septentrionale (L.) Hoffm.—Widely distributed on all slopes of the mountain at 7100–8700 ft elevation. The plants occupy a variety of habitats, but most are found in shaded cracks on exposed boulders and cliff faces. They appear to be morphologically indistinguishable from European specimens, and all sampled

sporangia contained 64 normal spores. A chromosome count of $n=72$ II (*Fig. 1D*) agrees with previous determinations in Eurasia (Löve, Löve & Pichi Sermolli, 1977) and the disjunct population in Monroe County, West Virginia (Emory, 1970).

Asplenium trichomanes L. subsp. trichomanes.—Found in deep cracks and crevices on all slopes of Elden Mountain at 7000–8300 ft elevation. Plants are closely associated with *A. platyneuron* in several places, but there is no evidence of local hybridization. Mature sporangia consistently produced 64 normal spores with a mean diameter of 28 μm. Moran (1982) assigned Arizona collections to the diploid cytotype on the basis of spore dimensions, and a chromosome count of $n=36$ II (*Fig. 1E*) substantiates his prediction.

Cheilanthes eatonii Baker—Discovered in 1978, this fern inhabits exposed ledges and cliffs on the southern and western slopes at 7000–8100 ft elevation. Considering its abundance on the south side of the mountain, it is surprising that the species was overlooked by previous collectors. Local materials have traditionally been assigned to forma *eatonii*, which exhibits a dense tomentum on the upper surface of the frond. All sampled sporangia yielded 32 large, well formed spores, suggesting that the plants are apogamous.

Cheilanthes feei Moore—Common on all slopes of the mountain, this species favors relatively dry, exposed cliffs at 7000–8500 ft elevation. The presence of 32 spores in each sporangium suggests that local plants are apogamous triploids similar to those studied by Knobloch (1967).

Cheilanthes fendleri Hook.—Discovered in 1978, the Elden Mountain population comprises at least 50 plants on the eastern, southern, and western slopes at 7200–8100 ft elevation. Most plants inhabit well shaded ledges on the eastern side of the mountain. All sampled sporangia contained 64 normal spores, and a chromosome count of $n=30$ II (*Fig. 1F*) is apparently the first report for the species.

Cheilanthes wootonii Maxon—Favoring shaded ledges on south-facing cliffs, this species is scattered over the eastern, southern, and western slopes at 7100–7700 ft elevation. Mature sporangia consistently produced 32 large, well formed spores. Meiotic squashes revealed that both apogamous and sexual pathways operate during sporogenesis, although the latter was rarely observed. Sporangia following the apogamous pathway contained eight large spore mother cells that showed $n=90$ II (*Fig. 1G*). Sporangia utilizing the sexual pathway contained 16 smaller spore mother cells at the beginning of meiosis. It was not possible to obtain an exact chromosome count on cells of this type, but several preparations suggest that $n=$ ca. 30 II + 30 I. Most univalents do not converge on the plate during metaphase, and the resultant unequal distribution of chromosomes leads to spore malformation. These data indicate that local plants of *C. wootonii* are apogamous triploids of hybrid origin. A Texas plant studied by Knobloch (1967) showed $2n=116$, suggesting that this polymorphic species includes at least two cytotypes.

Cystopteris cf. tennesseensis Shaver—Not previously reported for Arizona, although a number of pteridologists have been aware of its occurrence in the state (W. H. Wagner, pers. comm., 1982). The Elden Mountain colony is located ca. 700 km NW of the westernmost station in the Guadalupe Mountains of Texas (Blasdell, 1963). The species was originally collected by L. N. Goodding in 1913 and

identified as *C. fragilis*. Goodding's collection was overlooked by Phillips (1947) and omitted from his checklist of Arizona ferns. The population consists of ca. 35 plants growing on the western slope at 8000–8100 ft elevation. The plants are confined to seepage zones in deep crevices and cliff recesses; several grow in close proximity to the *Adiantum pedatum* colony. A sample of 20 sporangia was removed from two different plants, and 19 of them contained 64 normal spores. The remaining sporangium yielded 32 exceptionally large, well formed spores. Further study will be necessary to determine the viability and ploidy level of these unreduced products of sporogenesis. Chromosome counts of $n=84$ II (*Fig. 1H*) were obtained from sporangia with the normal complement of 16 spore mother cells. The presence of minute bulblets on some plants suggests that the species is an allotetraploid whose parentage includes *C. bulbifera*. The plants resemble typical *C. tennesseensis* in many respects, but the two taxa are probably not identical.

Dryopteris filix-mas (L.) Schott— This conspicuous fern is frequently collected and occurs on all slopes at 7100–8600 ft elevation. Its preferred habitat consists of shaded cracks and crevices with an ample supply of moisture. All sampled sporangia contained 64 normal spores, and a chromosome count of $n=82$ II (*Fig. 1I*) agrees with an earlier report from western North America (Reisender, 1974). The morphology of local specimens is highly variable, and fronds range from early deciduous to evergreen.

Pellaea truncata Goodding—Discovered in 1979, the Elden Mountain colony consists of ca. 10 plants growing on the eastern and southern slopes at 7400–7700 ft elevation. The species is rarely collected on elevated sections of the Colorado Plateau, and plants are confined to dry, south-facing cliffs and ledges. A sample of ten sporangia yielded nine with 64 spores and one with 32 exceptionally large spores that may be unreduced products of sporogenesis. A chromosome count of $n=29$ II (*Fig. 1J*) agrees with previous reports (as *P. longimucronata*) by Knobloch and Britton (1963). Most fronds tend to be tripinnate at the base, but local specimens are otherwise similar to their low elevation counterparts.

Pellaea wrightiana Hook.—Common on the eastern, southern, and western slopes of the mountain at 7000–8100 ft elevation. The habitat requirements of this species are nearly identical to those of *Cheilanthes eatonii*, and the two often grow together on the low cliffs of the southern slope. A sample of ten sporangia yielded nine with 64 spores and one with 32 exceptionally large spores. This situation is not unusual in *P. wrightiana*, and all Arizona collections thus far examined have produced similar ratios. A chromosome count of $n=58$ II (*Fig. 1K*) provides further support for Wagner's (1965) assertion that this taxon is typically a fertile tetraploid. Sterile triploid hybrids between this and the preceding species have been found on the southern slope at 7100 ft elevation.

Pityrogramma triangularis (Kaulf.) Maxon—Discovered in 1979, the Elden Mountain colony provides the first record for Coconino County and indicates that the species has a much greater elevation range than was previously suspected. The colony consists of three small plants growing from a permanently shaded crack on the southern slope at 7125 ft elevation. Mature sporangia consistently produced 64

normally-developed spores. Atypical morphology and a paucity of material preclude identification at the varietal level.

Polypodium hesperium Maxon—Found in shaded cracks and crevices on all slopes of the mountain at 7600–8700 ft elevation. All sample sporangia yielded 64 normal spores, and a chromosome count of $n=74$ II (*Fig. 1L*) agrees with previous Arizona reports by Knobloch (1962) and Lloyd (1963). Local plants have acrid, pruinose rhizomes that distinguish them from typical populations in the Pacific Northwest.

Polystichum scopulinum (D. C. Eaton) Maxon—Arizona lies at the southern distributional limit of this species, and most populations are small and sporadically distributed. The Elden Mountain colony is the largest in the state, including at least 250 individuals on the western, southern, and eastern slopes at 7100–8200 ft elevation. The plants favor shaded cracks and crevices on south-facing cliffs. All sampled sporangia contained 64 normal spores, and a chromosome count of $n=82$ II (*Fig. 1M*) agrees with previous determinations by Wagner (1973).

Pteridium aquilinum (L.) Kuhn var. pubescens Underw.—This widespread taxon is rarely observed on Elden Mountain and was not collected until 1979. It favors rocky soils in open coniferous forests, occurring on all slopes at 7000–7700 ft elevation. Chromosome and spore counts are not available because the population showed no evidence of sexual reproduction from 1979 to 1983.

Woodsia mexicana Fée—Common on the eastern, southern, and western slopes of the mountain at 7000–7600 ft elevation. The plants grow on partially shaded cliffs and ledges and are often associated with *Pellaea wrightiana*. All sampled sporangia yielded 64 normal spores, and chromosome counts of $n=76$ II (*Fig. 1N*) were obtained from five different plants. These counts conflict with Knobloch and Correll's (1962) report of $n=82$ and substantiate Brown's (1964) hypothesis that the species is a tetraploid based on $x=38$. Specimens from northern Arizona and New Mexico are somewhat atypical, showing substantial reductions in the length of both indusial filaments and marginal processes.

Woodsia oregana D. C. Eaton—All Elden Mountain collections of this species have previously been referred to *W. plummerae* (Phillips, 1947). The specimens are unusually glandular and their indusial segments tend to be united at the base. However, they bear little resemblance to typical *W. plummerae* of southern Arizona, and preliminary flavonoid data indicate that the two are biochemically distinct. Scanning electron microscopy has also revealed clear and consistent differences in spore ornamentation. Seven plants from Elden Mountain were examined cytologically, all of which yielded counts of $n=76$ II (*Fig. 1O*). Similar materials gathered from four other localities in northern Arizona also proved to be tetraploid. Overall morphology suggests a close relationship to *W. oregana*, but typical collections of that species are reportedly diploid (Brown, 1964). Additional data will be necessary to resolve the apparent discrepancy between morphology and cytology. The species is sporadically distributed on all slopes at 7000–8700 ft elevation. The plants are usually found in shaded cracks and crevices, and all sampled sporangia contained 64 normal spores. Sterile tetraploid hybrids between this and the preceding species have been found on the southern slopes of Elden Mountain at 7000 ft elevation.

The fern flora of Elden Mountain includes ca. 20% of the species known to grow in Arizona. Several are relatively common in the state, but *Asplenium adiantum-nigrum* and *A. platyneuron* are apparently confined to this locality. The number of xerophytic ferns is unusually high considering the elevation, and 40% of the taxa are rarely found north or west of Elden Mountain. Included in this category are *Asplenium resiliens, Cheilanthes eatonii, C. fendleri, C. wootonii, Pellaea wrightiana* and *Woodsia mexicana*. Four species (20%) are known or suspected apomicts, showing triploid chromosome numbers and 32 spores per sporangium. Local *Pteridium* colonies are strongly rhizomatous and they, too, form the bulk of their populations without sexual processes. Approximately 69% of the sexual species are tetraploids; the remainder are diploids. Several of the tetraploids are nothospecies of hybrid origin, including *Asplenium adiantum-nigrum, Cystopteris* cf. *tennesseensis, Pellaea wrightiana,* and *Polypodium hesperium*. In each case, one or both of the putative parents are absent from Elden Mountain and there is no evidence that the species were formed locally. However, interspecific hybridization is moderately common on the mountain, and sterile hybrids have been detected in both *Pellaea* and *Woodsia*.

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REVIEW

FERNS AND FERN-ALLIES OF MEGHALAYA STATE, INDIA, by A. K. Baishya and R. R. Rao. Scientific Publishers, Jodhpur, India. viii + 161 pp. 1982. Rs. 100.—Meghalaya State is a portion of what was formerly called Assam. It occupies more than 22,000 square kilometers and lies north of Bangladesh and south of the Himalayas in northeastern India. The topography is diverse and ranges from 100 to 1990 m in elevation. Vegetation types include evergreen and semi-evergreen forests, deciduous forests, subtropical pine forests, grasslands, and temperate forests. Terrestrial, lithophilic, and epiphytic ferns are found. The pteridophytes number 256 species in 91 genera, a rich and diverse flora. None of the genera has more than 20 species; the largest are *Selaginella* and *Asplenium*. The present volume includes keys to the families, genera, and species, synonymies, descriptions, habitat and range notes in the Flora area, an interesting introduction, a bibliography, and an index. Some of the species are illustrated with photographs or line drawings. The keys seem well constructed. The book will be of interest to all who deal with the ferns of India and the surrounding region. The book is available from United Book Traders, Opposite Police Lines, Ratanada, Jodhpur 342001, India. The U.S. price of $20.00 far exceeds the rupee price.—*D.B.L.*